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Rhythm makes the world go round: An MEG-TMS study on the role of right TPJ theta oscillations in embodied perspective taking

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Abstract

While some aspects of social processing are shared between humans and other species, some aspects are not. The former seems to apply to merely *tracking* another's visual perspective in the world (i.e., what a conspecific can or cannot perceive), while the latter applies to perspective *taking* in form of mentally "embodying" another's viewpoint. Our previous behavioural research had indicated that only perspective *taking,* but not *tracking,* relies on simulating a body schema rotation into another's viewpoint. In the current study we employed Magnetoencephalography (MEG) and revealed that this mechanism of mental body schema rotation is primarily linked to theta oscillations in a wider brain network of body-schema, somatosensory and motor-related areas, with the right posterior temporo-parietal junction (pTPJ) at its core. The latter was reflected by a convergence of theta oscillatory power in right pTPJ obtained by overlapping the separately localised effects of rotation demands (angular disparity effect), cognitive embodiment (posture congruence effect), and basic body schema involvement (posture relevance effect) during perspective *taking* in contrast to perspective *tracking*. In a subsequent experiment we interfered with right pTPJ processing using dual pulse Transcranial Magnetic Stimulation (dpTMS) and observed a significant reduction of embodied processing. We conclude that right TPJ is the crucial network hub for transforming the embodied self into another's viewpoint, body and/or mind, thus, substantiating how conflicting representations between self and other may be resolved and potentially highlighting the embodied origins of high-level social cognition in general.

Keywords (5): Perspective Taking, Embodiment, Magnetoencephalography (MEG), Transcranial Magnetic Stimulation (TMS), Temporo-Parietal Junction (TPJ)

Abbreviations: MEG = Magnetoencephalography; dpTMS = dual pulse Transcranial Magnetic Stimulation; pTPJ = posterior temporo-parietal junction

1. **Introduction**

Humans and other species are social animals and therefore require specific information processing capacities that ensure social functioning in cooperative and competitive situations. While some aspects of social processing are shared with other species, other aspects have only been observed in humans (Frith & Frith, 2007; Tomasello, Carpenter, Call, Behne, & Moll, 2005). The latter typically involves representing what others might be thinking or experiencing (Call & Tomasello, 1999), while the former relies on simpler and more automatic processing of others in relation to the environment (Kessler & Rutherford, 2010; Michelon & Zacks, 2006). In both cases, however, processing seems to ensure alignment of some sorts between agents, enabling coordinated social behaviour (Frith & Frith, 2007).

1.1. Perspective taking vs. perspective tracking

Simple alignment may take on the form of tracking another's perspective of the world, e.g. "Is the food visible or occluded from the view of the alpha male?" (Brauer, Call, & Tomasello, 2005, 2007). In contrast to other species, however, humans have the capacity to imagine another's perspective of the world (Call & Tomasello, 1999; Frith & Frith, 2007; Tomasello et al., 2005), e.g. when giving directions such as "turn left in front of the building". Such visuo-spatial perspective *taking* in form of imagining the world from another's viewpoint must be distinguished from merely *tracking* what a conspecific can or cannot see as observed in other species.

Nevertheless, apes and ravens have been reported to physically align themselves with humans, even moving around obstacles in order to be able to see what a human can see (Brauer et al., 2005; Bugnyar, Stöwe, & Heinrich, 2004). Such understanding of the required physical movement for aligning viewpoints could reflect a proto-form of higher-level perspective *taking*. If this was the case, then perspective taking in humans may have evolved from physical viewpoint alignment, in other words, a mental simulation of adopting another's viewpoint may have replaced actual movement execution.

1.2. The embodied nature of perspective taking

An increasing number of research findings indeed show that perspective taking is linked to internal representations of the body and its action and posture repertoire (Falconer & Mast, 2012; Surtees, Apperly, & Samson, 2013; Tcaci Popescu & Wexler, 2012; Tversky & Hard, 2009; van Elk & Blanke, 2014). Kessler and Thomson (2010) directly manipulated participant's body posture during perspective taking (Fig. 1): When the body was turned towards the target (posture "congruent" with the direction of mental self-rotation), response times and error rates for directional judgments ("left/right") from another's perspective were significantly decreased compared to when the body was turned away ("incongruent" posture). This effect has been repeatedly replicated and extended (Kessler & Rutherford, 2010; Kessler & Wang, 2012; Surtees et al., 2013; Tcaci Popescu & Wexler, 2012; van Elk & Blanke, 2014) and suggests that high-level visuospatial perspective taking is indeed based on a simulated rotation of the body (Kessler & Wang, 2012). Importantly, Kessler and Rutherford (also Kessler, Cao, O'Shea, & Wang, 2014; 2010) showed that during simple perspective *tracking* (judging "visibility") the posture congruence effect was absent. This suggests that only the more complex process of perspective taking is significantly "embodied", in the sense that humans mentally rotate their own body representation into another's orientation in form of a mental self-rotation.

1.2. The role of the temporo-parietal junction

Previous research in social cognitive neuroscience has implicated the temporo-parietal junction (TPJ) as a crucial area within a network generally engaged when inferring others' experiences and mental states (Arzy, Thut, Mohr, Michel, & Blanke, 2006; O. Blanke et al., 2005; Bögels, Barr, Garrod, & Kessler, 2014; Van Overwalle & Baetens, 2009; Zacks & Michelon, 2005) and particularly during high-level visuospatial perspective taking (Arzy et al., 2006; O. Blanke et al., 2005; Bögels et al., 2014). Recent structural and functional investigations suggest subdivisions of TPJ along an anterior-posterior and a ventral-dorsal dimension (Igelström, Webb, & Graziano, 2015; Mars et al., 2012). Converging results seem to indicate that a posterior section of TPJ is particularly linked to social processing (Carter & Huettel, 2013; Igelström et al., 2015; Mars et al., 2012).

A variety of notions have been proposed for the role of TPJ involvement, e.g. suggesting a role in spatially transforming frames of reference or in simultaneous co-representation of several frames of reference (Schurz, Aichhorn, Martin, & Perner, 2013). It has further been proposed that especially the right TPJ controls conflicting representations of the self in relation to others, such as suppressing the self when the other's representation is task-relevant and vice versa (Santiesteban, Banissy, Catmur, & Bird, 2012). However, work by Blanke and colleagues (Arzy et al., 2006; O. Blanke et al., 2005) using transcranial magnetic stimulation (TMS) and testing a patient suffering from involuntary "out-of-body" experiences, supports the notion that processing in TPJ could be related to bodily representations and not merely to abstract spatial processing. Indeed, based on lesion studies, areas in the parietal cortex including the TPJ (G. Berlucchi & Aglioti, 1997; Giovanni Berlucchi & Aglioti, 2010; O. Blanke et al., 2005; Buxbaum, Giovannetti, & Libon, 2000; Tsakiris, Costantini, & Haggard, 2008; Wolpert, Goodbody, & Husain, 1998) have been associated with the so-called "body schema", which has been defined by Coslett and colleagues (e.g. Coslett, Buxbaum, &

Schwoebel, 2008; Medina, Jax, & Coslett, 2009) as a continuously updated, dynamic representation of body part locations based on proprioceptive and efference-copy information.

1.2. The current study

Here we employed the novel paradigm and posture manipulation from Kessler and Rutherford (2010) and expected overlapping effects in the TPJ between visuospatial and body-related transformations during a perspective *taking* task, in contrast to a perspective *tracking* task. A confirmatory result would highlight TPJ as the major network hub for embodied perspective transformations and would allow for unique conclusions about the type of processing carried out within TPJ and its recently proposed subdivisions (Carter & Huettel, 2013; Igelström et al., 2015; Mars et al., 2012). Potentially, this could substantiate a self-other control mechanism proposed for right TPJ (Santiesteban et al., 2012). Such a result would further emphasise the embodied origins of social cognition, suggesting that humans may have developed the capacity for mental alignment by engaging the body representation system in simulation mode (Gallese, 2013; Pezzulo, Iodice, Ferraina, & Kessler, 2013; Wilson, 2002). This capacity may come with a trade-off in the form of spontaneous, uncontrolled disembodiment, that has also been linked to TPJ, hence, our findings could potentially further elucidate the link between perspective taking and spontaneous out-of-body-experiences (O. Blanke et al., 2005; O. Blanke & Thut, 2007; Braithwaite et al., 2013).

2. Materials and Methods

2.1 Participants

14 participants were tested in the MEG experiment at Glasgow University while a different group of 15 participants were tested in the TMS experiment at Aston University.

We obtained analysable MEG data from 12 participants (6 males, average age 23.3, all right-handed). Data from two additional participants was excluded because of too noisy data (dental implant), and for being on medication, respectively. All participants had a maximum score of 5 on the "social skills" subscale of the Autism-Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), based on our previous research showing that low social skills (indicated by larger values) may result in the engagement of alternative processing strategies (Kessler & Wang, 2012).

In the TMS experiment 15 volunteers participated (6 males, average age 26.3, minimum 21 and maximum 37, 3 left-handed). All participants were screened for contra-indications (Keel, Smith, & Wassermann, 2001) and had a maximum score of 5 on the "social skills" subscale of the Autism-Spectrum Quotient (Baron-Cohen et al., 2001).

2.2 Experimental Procedures

All experimental procedures complied with the Declaration of Helsinki and were approved by the respective University ethics committee.

2.2.1. MEG Expt.

The employed tasks and stimuli were adopted from Kessler and Rutherford (2010, Expt. 1). In all stimuli an avatar was presented seated at a round table shown from one of six possible angular disparities (see Figure 1: 60°, 110°, 160° clockwise and anticlockwise). The stimuli were coloured photographs (resolution of 1024 by 768 pixels), taken from an angle of 65° above the plane of the avatar and table. The stimulus table contained four grey spheres (placed around an occluder, cf. Figure 1). In each trial one of the spheres turned red indicating this sphere as the target. From the avatar's viewpoint the target could be visible/occluded (perspective *tracking* task) or left/right (perspective *taking* task) and participants were asked to make a judgement according to the avatar's perspective by pressing the instructed key (Lumitouch® response pads): the left key for "left" or "visible" targets and the right key for "right" or "occluded" targets[1]. For analysis we collapsed across correct responses for left and right and across correct responses for visible and occluded, respectively. We also collapsed across clockwise and anticlockwise orientations for each angular disparity, after ensuring that the neural signatures were comparable (no significant differences in source space).

For each block of 120 trials (8 total per session) participants were instructed to maintain one of two possible postures as shown in Fig. 1, bottom right. The participant's posture in any given block was always congruent with the mental rotation direction required for half of the trials, while it was incongruent with the other half. A blocked posture was essential for avoiding movement artefacts in the MEG due to inter-trial posture adjustments. The two tasks (perspective taking vs. tracking) were recorded in two separate sessions on different days and the sequence was counterbalanced across participants.

MEG data were acquired using a Magnes 3600, 248-channel whole-head magnetometer (4D-Neuroimaging), sampled at 508.63 Hz and band-pass filtered between 0.1 and 200 Hz. Stimulus resolution was 1024 x 768 pixels covering a visual angle of 24º horizontal by 18º vertical. We employed an SR Research remote Eyelink 1000 fort aborting trials (to be re-run

[1] Note that in Kessler and Rutherford (2010) we found the same basic pattern of results with vocal responses ("left" or "right" for perspective taking and "in front" or "behind" for perspective tracking) as with spatially mapped key presses. This is important as vocal responses do not induce spatially incongruent stimulus-response mappings (see May & Wendt, 2013). Thus, since our current study replicated the pattern reported in Kessler and Rutherford (2010) we are confident that our effects are not due to spatial incompatibilities in stimulus-response mappings (see also Kessler et al., 2014). Furthermore Surtees et al., (2013) reported a similar posture congruence effect in a task that did not require laterality judgements but judgements of visual appearance (e.g. does the other person perceive a digit as a "9" or a "6"?). This further rules out stimulus-response mappings as a confound but also indicates that the posture effect is not only tied to left/right or other directionality judgements but generalises to judgements of visual experience.

later) where participants blinked or moved their eyes away from the screen centre (a box of dimensions 140x120 pixels, covering the central target area, see Fig. 1).

Data were preprocessed & analysed using the Matlab® toolbox Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). Epochs were extracted from 600 ms before the visual stimulus was shown until response. All epochs were detrended, denoised and trials with large artefacts (e.g. strong muscle artefacts) and continuously noisy channels were removed (with max 6 out of 248 rejected channels and an average of 142.6 remaining trials per individual). ICA components were then generated, visually inspected and removed if they reflected environmental noise and/or artefacts (such as heart beats and muscle artefacts).

The power of frequencies between 2 and 32 Hz was calculated using a Hanning taper (Grandke, 1983) with 3 cycles per frequency. Planar gradient representations were calculated prior to sensor level analysis that used cluster-based random permutation (Maris & Oostenveld, 2007). Conforming to our previous research (e.g. Bögels et al., 2014) we employed a 2-step approach for emulating the interactions between two factors in time and frequency analysis (e.g. task x posture; task x angle). We first calculated differences between the two tasks, i.e. perspective *tracking* vs. *taking*, for each participant separately and then included the outcomes of this 1st step difference into a group statistic that compared a second factor, e.g. congruent vs. incongruent posture (or 60º vs. 160º). The comparison at group level followed the robust statistics approach described above. For localising the power of theta-band oscillations, we used the Dynamical Imaging of Coherent Sources (DICS, Gross et al., 2001) approach for calculating spatial filters based on cross-spectral densities for a time-frequency tile centred on the effects found at sensor level (3, 4, 5, 6 Hz; 0-660 msec).

2.2.2. TMS Expt.

The stimuli were identical to the MEG experiment but we simplified the paradigm by excluding trials with 110° angular disparity and by excluding visibility judgements in order to focus on the postulated pTPJ involvement in perspective taking. In addition, we randomly included trials with and without dual pulse TMS stimulation, hence, a 2x2x2 repeated measures design was employed with the factors “angular disparity” (160°/60°), “posture congruence” (congruent/incongruent), and “stimulation” (dpTMS vs. control). The total number of 160 trials (20 trials in each of the 8 design conditions) was delivered in 10 blocks of 16 trials each =, where participants maintained the same body posture (turned clockwise or anticlockwise, cf. Fig. 1 bottom right) throughout each block.

TMS was applied using a Magstim Super Rapid with a 70mm diameter figure-of-eight stimulating coil, with maximum magnetic field strength of 1.5T. Prior to the experiment three-dimensional brain models were created for each participant in neuronavigation software (BrainSight® v2, Rogue Research, Montreal, Canada), using each participants’ structural MRI that was normalised into MNI space (Montreal Neurological Institute template) with SPM8 software (Litvak et al., 2011). The target sites for stimulation were defined in normalised stereotactic space (MNI) and the coordinates were based on the MEG group analysis (MNI coordinates: 50, -60, 32) reflecting a right posterior temporo-parietal (pTPJ) site. Brainsight® hard- and software ensured continued accuracy of pulse application. Dual pulse TMS (dpTMS) was applied to right pTPJ in concordance with previous research targeting the TPJ (e.g. Bosco, Carrozzo, & Lacquaniti, 2008). Conforming to one of Bosco et al.’s (2008) conditions, the two pulses were separated by 100ms with the 1st pulse being administered at 300ms after stimulus onset (2nd pulse at 400ms). Bosco et al suggested that this would cause interference lasting for approx. 300-500ms after stimulus onset. This period further overlapped with the time window (350-550ms) reported by Blanke et al. (2005), where single pulse TMS affected perspective taking, and importantly, also covered the peak of the theta (and alpha/beta) effects observed in the current MEG experiment (200-400ms, Fig. 3, bottom). dpTMS was applied on 50% of the trials and pulses were applied at 110% resting motor threshold as determined in concordance with standard protocols (Rossini et al., 1994). On all trials (also on those without dpTMS stimulation) acoustic click sounds played binaurally via ear phones ensured that participants could not distinguish between dpTMS and control trials based on the sounds of the TMS coil discharge alone.

3. Results

3.1. MEG Experiment: Behaviour

Response time data (RTs) shown in Figure 2 were subjected to an ANOVA that included angular disparity (60°, 110°, 160°) posture congruence (congruent vs. incongruent), and task (left/right vs. visibility) as factors (see also Fig. 1). Based on previous research (Kessler et al., 2014; Kessler & Rutherford, 2010; Michelon & Zacks, 2006; Surtees et al., 2013), only for perspective *taking* (left/right) but not for perspective *tracking* (visibility) RTs were expected to slow down with increasing angular disparity as a reflection of increased duration of mental transformation. Only for perspective *taking* (left/right) but not for perspective *tracking* (visibility) RTs were also expected to be faster for a congruent than for an incongruent body posture as a reflection of body schema involvement in the mental transformation (Kessler et al., 2014; Kessler & Rutherford, 2010; Kessler & Thomson, 2010; Surtees et al., 2013).

Conforming to these expectations, the current results replicated Kessler and Rutherford’s findings (Kessler et al., 2014; 2010), revealing a significant main effect of angular disparity

(F(2,10) = 14.8, p<.001, η^2_p=.747) for perspective taking (left/right), where RTs increased with angle, and a main effect of posture congruence (F(1,11) = 10.1, p<.01, η^2_p=.478), with a congruent posture being significantly faster than an incongruent posture. In contrast, perspective tracking (visibility) only revealed a significant effect for angular disparity (F(2,10) = 12.2, p<.002, η^2_p=.71), yet, where RTs decreased with angle (Kessler et al., 2014). Significant interactions for task x angle (F(2,10) = 17.9, p<.001, η^2_p=.782), for task x posture (F(1,11) = 9.3, p<.01, η^2_p=.458) and for task x angle x posture (F(2,10) = 25.9, p<.001, η^2_p=.839) confirmed the qualitative difference between the two tasks, as suggested by previous research (Kessler et al., 2014; Kessler & Rutherford, 2010; Michelon & Zacks, 2006).

3.2. MEG experiment: Time-frequency results for theta, alpha, beta

We replicated the pattern of behavioural results reported in Kessler and Rutherford (Kessler & Rutherford, 2010) with posture congruence and angular disparity effects for left/right, but no such effects for visible/occluded judgements (as confirmed by significant interactions with "task"). This indication of more intense embodied processing and higher rotation demands during perspective taking compared to tracking was also reflected in the MEG data where we did not find any effect that was stronger for visibility compared to left/right judgements, when we compared the two tasks directly (see also Fig. 3, Panel A). Also note that when tested separately for each task, posture congruence and angular disparity revealed significant clusters for perspective taking but not for tracking (Fig. 3 Panel B). Therefore, to complete the overall picture we explored visibility judgments as a simple comparison between pre-stimulus baseline vs. post-stimulus task period (collapsed across all angular disparity and posture congruence conditions). This analysis is reported in the Supplementary Material (Fig. S1) and, in short, we observed significant effects in alpha, beta, and theta frequencies, indicating more intense processing during stimulus presentation compared to pre-stimulus baseline. Importantly, theta power differences localised in the frontal eye fields (FEF), which has previously been related to visibility judgements (Wallentin, Roepstorff, & Burgess, 2008) as well as to perceiving another's gaze and line-of-sight (Grosbras, Laird, & Paus, 2005).

Furthermore, we focussed our analysis of rotation demands on the maximum angular disparity difference of 160º vs. 60º, since 110º revealed a pattern that was in-between the two other angular disparities, thus, not adding fundamentally new insights. 110º did not differ significantly from the other two angular disparities at theta but at alpha/beta frequencies, which is reported in Supplementary Material Figure S2.

Conforming to the observed behavioural interaction effects of task x posture congruence and task x angular disparity, the main time-frequency (TFR) results were revealed in 2-level analysis approaches (e.g. Bögels et al., 2014), comparing the two tasks at individual level and then calculating an angle or posture effect at group level, thus, approximating the interactions between task x angle and task x posture congruence, respectively, while allowing for robust random-permutation cluster statistics to control for multiple comparison errors (see Section 2.3.). A data-driven analysis of frequencies between 2-32 Hz (see Section 2.3.) was calculated conforming to this 2-level analysis approach. Generally, all conditions followed a similar pattern of post-stimulus theta-band (2-7 Hz) increase and an alpha/beta-band decrease (8-25Hz) compared to baseline (see Fig. 3, Panel A). These are typical observations (Klimesch, 1999; Pfurtscheller & Lopes da Silva, 1999) associated with processing of incoming stimuli (alpha/beta decrease) that also require cognitive processing (theta increase). Although the general pattern and topography was similar for both tasks (see Fig. 3, Panel A), perspective taking (left/right) revealed by far the stronger responses, i.e., theta increases as well as alpha/beta decreases (see Differences in the far right column of Fig. 3, Panel A). In fact, we did not find any effect that was stronger for visibility compared to left/right judgements (but see Figure S1 for visibility judgements compared to the baseline interval). Furthermore we found the most reliable effects across all contrasts in the theta band incl. higher delta frequencies (2-7 Hz). We therefore focus our report on these frequencies but report additional alpha/beta effects in Supplementary Material (Figure S3).

It is important to note that comparing the two tasks in the MEG analysis provided us with a further contrast option that could not be conducted based on behavioural responses alone, or by analysing the tasks separately. Specifically, we were able to test if posture, disregarding congruency with the cognitive target at hand, mattered more for perspective *taking* than for perspective *tracking*. This directly relates to our general hypothesis that the body schema would be engaged during perspective taking but not during tracking: If that was the case, then the neural representation of posture should be more strongly engaged during left/right than during visibility judgements. It is safe to assume that a body turned clockwise vs. anticlockwise results in different neural representations that code for the two different postures. If a particular context is likely to use these posture representations on every given trial of a block, e.g. a block of left/right judgements, then the neural differences between the two postures should be enhanced compared to a block where posture is irrelevant, e.g. a block of visibility judgements. Hence, if posture was more relevant during left/right compared to visibility judgements, then we expected to find a stronger difference between the two body postures (body turned clockwise vs. anticlockwise, see Fig. 1) in the former compared to the latter, resulting in what we termed a "posture relevance" effect. To clarify, posture relevance is different from posture congruence in that it is likely to reflect a tonic activity increase related to the body schema for the left/right compared to the visibility task (presented in separate blocks), disregarding specific trial parameters such as mental rotation direction, demands and congruence[2].

The interaction between task and angular disparity was calculated for the maximum difference in angle, i.e., between 160º and 60º degrees, and revealed a significant cluster ($p < .05$; Fig. 5, left column) in the theta band (2-7Hz), lasting from 0ms to 650ms (Fig. 4, left). The 160º condition revealed a stronger theta increase than 60º (for left/right but not for visibility). The interaction between task and posture congruence was reflected by a significant cluster ($p < .05$) in the theta band (3-7Hz) and lasted from 50ms to 450ms (Fig. 4, middle column). In reflection of the obtained behavioural effects (see Fig. 2) posture congruence effects differed significantly between left/right and visibility judgements, with only the former showing significantly stronger theta modulation in response to posture incongruence vs. congruence. We also observed the predicted "posture relevance" effect where the two postures differed more strongly for left/right compared to visibility judgements, resulting in a significant cluster ($p < .05$) in the theta band (2-7Hz) that lasted from 0ms to 650ms (Fig. 4, right column). This effect, reflecting higher relevance of posture for left/right than for visibility judgements, further supports stronger engagement of the body schema during perspective taking (left/right) compared to mere perspective tracking (visibility). Finally, the effects for all three interactions seem to overlap over the right posterior hemisphere (Fig. 4, bottom row), possibly indicating a source in the right TPJ.

3.3. MEG experiment: Source analysis for theta

Figure 4 (middle row and top image) depicts the source reconstructions for each of the three theta interaction effects (with task) obtained with a similar 2-level approach as for the sensor

[2] Posture relevance was calculated as (L/R (anticlockwise) – visibility (anticlockwise)) - (L/R (clockwise) – visibility (clockwise)), while posture congruence as (L/R (incongruent) – visibility (incongruent)) - (L/R (congruent) – visibility (congruent)).

level analysis (see Section 2.3.); the source coordinates in MNI space are provided in Table 1. Firstly, angular disparity localised in the posterior part of the right TPJ (pTPJ), extending dorsally into dorsal TPJ and ventrally into the lateral occipital complex, overlapping with the extrastriate body area (OCC). More anterior sources include sensorimotor (SM1) and frontal areas (SMA, latPFC), thus, reflecting the topography of the widely distributed sensor level cluster (Fig. 4, bottom left). Secondly, posture congruence (Fig. 4, bottom middle; Table 1) also localized in the right pTPJ extending into more superior areas of the posterior parietal lobe (SPL) as well as to the right supplementary motor area (SMA). The posture relevance effect also localised in the right pTPJ (Fig. 4, bottom right; Table 1) along with right sensorimotor (SM1) and ventral premotor cortex (vmPFC). Finally, Figure 4 and Table 1 reveal that the maximum overlap between the three effects is indeed located in the right pTPJ, thus confirming our hypothesis that TPJ could be the locus where the embodied self is transformed into another's perspective and experience, possibly aligning bodies as well as minds.

3.4. TMS experiment: effects of dpTMS applied to rTPJ

We tested the proposed critical role of right pTPJ for embodied processing during perspective taking (left/right). We targeted the right pTPJ with a dual pulse TMS paradigm (dpTMS; e.g. Bosco et al., 2008) based on the coordinates obtained from the MEG overlap analysis (Fig. 4, top; Fig. 5, left) and the time window observed for the theta effects (Fig. 3) and in concordance with previous research (see Methods). We applied the 1st pulse at 300 and the 2nd pulse at 400 msec after stimulus onset. On all trials acoustic click sounds, mimicking TMS coil discharges, were played via ear phones. The played sounds were louder than the actual discharges; hence, participants were unable to distinguish acoustically between dpTMS trials and no-pulse control trials, which allowed us to mix TMS and sham trials into a random trial-sequence. The binaurally played sounds also masked the spatial asymmetry of the real coil discharges over the right hemisphere, which otherwise could have resulted in a spatial bias to the right.

The factor "stimulation" (dpTMS vs. control) was included as a within-subjects factor into a 2x2x2 repeated measures ANOVA along with the factors "angular disparity" (60º vs. 160º) and "posture congruence" (congruent vs. incongruent). The analysis revealed a significant main effect of "angular disparity" ($F(1, 14) = 20.6$, $p < .0001$, $\eta^2p = .595$), a significant interaction between "angular disparity" and "posture congruence" ($F(1, 14) = 7.8$, $p = .014$, $\eta^2p = .359$), and a significant interaction between "stimulation" and "posture congruence" ($F(1, 14) = 6.5$, $p = .023$, $\eta^2p = .319$). All other effects did not reach significance (all $p > .1$). The first two effects are in line with our previous research showing faster RTs at low (60°) compared to high (160°) angular disparity and a significant posture effect at high (160°) but not at low (60°) angular disparity (Kessler & Thomson, 2010; Kessler & Wang, 2012). The third effect is novel and can be interpreted, based on Fig. 5 (right graph), as a disruption of the posture congruence effect by dpTMS to right pTPJ. Although the 3-way interaction between angle, posture, and stimulation was not significant ($p = .381$), Fig. 5 (right graph) reveals that dpTMS primarily disrupted the posture effect where it existed in the first instance, namely at 160°.

4. Discussion

Firstly, our current MEG Expt. replicated previous behavioural findings (Kessler et al., 2014; Kessler & Rutherford, 2010; Kessler & Thomson, 2010; Kessler & Wang, 2012; Surtees et al., 2013) showing a significant RT increase (Fig. 2) in relation to higher angular disparity and posture incongruence for perspective *taking* (left/right) in contrast to perspective *tracking* (visibility), hence, further corroborating the notion of two distinct mechanisms (Michelon & Zacks, 2006). One mechanism seems to be restricted to the simpler process of tracking another's line of sight, while the other allows for imagining another's perspective by engaging an embodied process of mental self-rotation into the other's orientation (Kessler et al., 2014; Kessler & Rutherford, 2010; Michelon & Zacks, 2006). This clear behavioural pattern (i.e., posture and disparity effects only in the left/right task) allowed us to pursue the neural substrate of perspective taking (left/right) in comparison to perspective tracking (visibility). While all reported effects in the direct task comparison were indeed due to stronger oscillatory modulation in the left/right task, we were nonetheless able to pinpoint FEF as a major processing hub for the visibility task compared to a pre-trial baseline period (2-7 Hz, see Fig. SM1), replicating previous findings (Grosbras et al., 2005; Wallentin et al., 2008) and, thus, confirming a potential role of FEF in inferring another's line of sight .

Regarding perspective taking (in contrast to *tracking*) our data-driven time-frequency analysis revealed that modulations of theta oscillations were a common theme (Fig. 4, bottom row) amongst our three types of effects,. "Rotation demands" was reflected in higher theta power for 160° vs. 60° angular disparity, "cognitive embodiment" was reflected by stronger theta for an incongruent vs. a congruent posture, and "posture relevance" was reflected by a stronger theta contrast between anti- vs. clockwise turned body postures for perspective taking compared to tracking. Not only was the frequency of interest (~2-7 Hz) in common across all three effects, but also the primary cortical origin of these effects overlapped in the right posterior temporo-parietal junction (pTPJ; Fig. 4 top image). This is in agreement with previously reported involvement of right TPJ-theta in high-level perspective taking and mentalizing (Bögels et al., 2014). In the subsequent TMS study we were able to disrupt the posture congruence effect ("cognitive embodiment") by targeting right pTPJ with a dual pulse interference paradigm (Fig. 5). However, we did not find a dpTMS effect on angular disparity indicating that rotation demands were unaffected by the stimulation. A more disruptive repetitive TMS protocol might have affected both effects. However, our result could also be related to the targeted site being drawn more towards the body-related effects in the overlap (Fig. 4). Potentially, it might be possible to selectively disrupt the effects of posture or angular disparity or both, by targeting slightly different sites within right TPJ.

4.1. Implications for the role of TPJ

Our findings are in concordance with previous research that has pinpointed TPJ, and pTPJ in particular, as a crucial area within a network generally engaged when inferring others' experiences and mental states (Arzy et al., 2006; O. Blanke et al., 2005; Bögels et al., 2014; Van Overwalle & Baetens, 2009; Zacks & Michelon, 2005). In addition, TPJ has also been related directly to high-level visuospatial perspective taking and notions of the role of TPJ either suggest an embodied contribution (Arzy et al., 2006; O. Blanke et al., 2005) or the deliberate transformation of frames of reference and/or the co-representation of egocentric and altercentric perspectives (e.g., Santiesteban et al., 2012; Schurz et al., 2013). However, TPJ does not seem to be confined to deliberate processing of another's experience but has also been associated with spontaneous forms of viewpoint changes, prominently subsumed under the label of "out-of-body" experiences (Blanke et al. 2005; Braithwaite et al. 2010; Braithwaite et al. 2013), which is supportive of body-related processing in TPJ.

Our current empirical evidence allows reconciling diverging views of the role of TPJ by suggesting it as the locus of convergence between implicit body representation, i.e. the body schema (e.g. Coslett et al., 2008; Medina et al., 2009), and deliberate processes that use simulated manipulations of these representations to imagine the body (and mind) in another('s) viewpoint. This has implications on how the self is represented in relation to another. Previous research (Santiesteban et al., 2012) had proposed that TPJ controls conflicts between representations of the self- in contrast to representations of another. Santiesteban et al. (2012) reported TPJ involvement when "the other" needed to be ignored while focussing on the self (e.g. supressing automatic imitation tendencies), yet also when self-centred representations needed to be supressed to represent the other (e.g. when adopting the other's perspective). Our current findings extend and substantiate this rather vague notion of self- vs. other representations. As explained, our findings suggest that humans simulate a rotation of their embodied self into the other's orientation. Thus, we propose that a conflict arises because of a simulated self where parts of the body schema have been rotated outside the current location of the body, while parts of the self and the body schema remain tied to the body's current physical location (see also May, 2004). Without the latter mental self-rotation would always result in full-blown "out-of-body" experiences.

Therefore, our notion shifts the focus away from "the other", towards conflicts that arise between alternative (physically vs. mentally embodied) representations of the self. This implies that humans might represent others primarily by generating an alternative representation of the self in the other's circumstances (e.g. their body posture, viewpoint, perspective, socio-emotional context, etc.; e.g. Pezzulo et al., 2013). Accordingly, TPJ might play a crucial role in simulating projected selves and controlling conflict with the self that remains in the physical location of the body. This shift away from "the other" towards alternative embodied selves is corroborated by the role of TPJ in "out-of-body" experiences (e.g.O. Blanke et al., 2005), where an alternative embodied self is generated while no other is present. Furthermore, in our previous research using the same basic paradigm as reported here we substituted the avatar, i.e. "the other", with an empty chair, where participants had to imagine themselves being located, while making left/right judgments towards target objects (Kessler & Thomson, Expt. 2). Importantly, the basic mechanism of embodied mental self-rotation was also engaged in this version without avatar, as suggested by typical effects of posture congruence and angular disparity. This further corroborates our notion of a body-schema-related conflict in TPJ between a projected self (via simulated body-schema rotation) and the self that remains physically embodied (May, 2004 proposes a similar notion, but see Kessler & Thomson, 2010, for discussion). Sometimes during “out-of-body” experiences individuals report that they perceive their self as being embodied in two locations at the same time (so-called heautoscopy; O Blanke & Mohr, 2005). This indicates that the proposed split of the self is possible and while it is being perceived as odd, when it is triggered uncontrollably, it may serve the crucial purpose of perspective taking, when it is engaged deliberately. Indeed, our recent research confirms that individuals who report “out-of-body” experiences are quicker at mentally adopting another’s body orientation (Braithwaite et al., 2013).

4.2. TPJ linking separate functional subnetworks

In addition to the convergence of theta effects in right pTPJ, we also observed differences in theta power localisation for the three effects (Fig. 4, middle row). For rotation demands (160° vs. 60° angular disparity) we observed a more widely distributed topography (Fig. 4, bottom left), which could reflect executive function (latPFC) as well as visual processing (OCC) in a theta-based network of brain areas. The lateral occipital source overlaps with the extrastriate body area (EBA) and suggests more intense visual processing of the avatar’s body (for review, Carter & Huettel, 2013), when rotation demands are higher (160° vs. 60°). In Kessler & Thomson (2010, Expt. 4; also Kessler & Rutherford, 2010) we had argued that the presence of another’s body and their posture helps determining the accurate endpoint of the mental self-rotation process - particularly at high angular disparities. Sustained theta activation in the EBA observed here corroborates this notion of another's body as an important visual parameter for mental self-rotation. For the effect of angular disparity, right TPJ activation extends into dorsal TPJ which has previously been related to executive functions (Igelström et al., 2015; Mars et al., 2012). Overall the source configuration for the angular disparity effect fits well with our interpretation that it might reflect rotation demands that engage executive functions and rely on rotation parameters.

Theta power effects for posture congruence localised in right pTPJ and further areas within the superior parietal cortex (BA 40/7) that have been associated with sensorimotor representations and the body schema (Andersen, Snyder, Bradley, & Xing, 1997; Wolpert et al., 1998). Activation of the pTPJ extends ventrally into EBA, further underlining processes that integrate the perception of another's body (i.e. the avatar in the scene) with the process of transforming the embodied self into the other's orientation. Again, this dovetails nicely with our previous behavioural findings (Kessler & Thomson, 2010, Expt. 4), where we demonstrated an accelerating effect on perspective taking if the avatar's body posture matched the participants' posture. This emphasises the importance of another's posture for perspective taking, not only as a visual parameter for rotation, but also by generating embodied resonance between participant and avatar.

The emerging picture of the neural signature of embodied mental self-rotation is completed by the sources for the "posture relevance" effect, where stronger body schema involvement during perspective taking compared to tracking was reflected by localisations in right pTPJ and right ventrolateral premotor (vPMC) and sensorimotor (SM1) areas. This could directly reflect the embodied simulation process postulated for perspective taking. It is unlikely that this localisation is due to the preparation of a motor response (key press), since equivalent preparation processes could be expected for all conditions. vPMC specifically has been associated with embodied simulations and re-enactment in social interaction (Gallese, 2013; Wheatley, Milleville, & Martin, 2007) and our results emphasise the integration with TPJ for simulating a body rotation into another's viewpoint, possibly along with sensorimotor feedback from the simulation (e.g. Tcaci Popescu & Wexler, 2012) and/or sensorimotor conflict between physically vs. mentally embodied self. Overall our findings corroborate the notion of a simulated body rotation that generates an updated efference copy within the body schema, which in turn drives the actual visuospatial transformation process (Kessler & Thomson, 2010; Tcaci Popescu & Wexler, 2012; Zacks & Michelon, 2005).

4.3. Implications for the wider context of social processing

Within a wider context our current findings and our previous research suggest that high-level perspective taking is still grounded in older action- and body-related brain systems, in other words, that older systems have been re-purposed for resolving new challenges (see also Gallese, 2013; Kessler & Thomson, 2010; Parkinson & Wheatley, 2013; Pezzulo et al., 2013; Wilson, 2002). This could explain the evolution of perspective taking from physical alignment that is observed in other species (Kessler & Thomson, 2010). More generally, the embodied origin of mentalizing could be reflected by TPJ activation in conjunction with other body-related brain areas. This notion of visuo-spatial perspective taking as a developmental and possibly evolutionary stepping stone for full-blown theory of mind has recently found agreement (Hamilton, Brindley, & Frith, 2009; Parkinson & Wheatley, 2013) as well as disagreement (Moll & Kadipasaoglu, 2013), where the latter postulates that social empathy and perspective understanding precedes visuo-spatial perspective taking. While we believe that our findings rather support the former, we acknowledge that certain forms of joint attention may predate even simple perspective tracking.

5. Conclusions

Significant aspects of information processing in humans are not shared with other species. In the social domain such processes have been typically related to explicitly representing the subjective experience and mental states of others. However, some of these unique abilities still seem to depend on “older” systems such as the body’s movement repertoire. The current research confirmed that the human capacity for imagining another’s perspective of the world is still significantly “embodied”, in the sense that humans mentally rotate their own body representation (body schema) into another’s orientation. Using Magnetoencephalography we found that brain oscillations at theta frequency, originating from the right posterior temporo-parietal-junction (pTPJ) reflected cognitive as well as embodied processing elements. This was subsequently confirmed using transcranial magnetic stimulation, which disrupted embodied processing effects, pinpointing right pTPJ as the crucial network hub for transforming the embodied self into another’s viewpoint, body and/or mind. We propose that such a “transformed embodied self”, projected into another’s circumstances (e.g. their posture, orientation, perspective, socio-emotional context, etc.), serves as the basis for representing and understanding others in various social scenarios. Using state-of-the-art methodology our research elucidates the embodied origins of high-level social processing in humans, specifically highlighting the critical role of right pTPJ and theta oscillations.

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Table 1. Labels, Brodmann areas, and MNI coordinates for sources identified in Figure 4.

ource label in ig. 4	Brodmann Areas	Brain areas	MNI Coordinates		
) Contrast for Angle (160º vs. 60º)					
pTPJ	39/7	Right temporo-parietal junction: angular gyrus	34	-70	44
OCC	18/19	Right occipital cortex/lateral occipital complex	26	-90	0
infSMG	2/40	Right supramarginal gyrus	64	-22	32
SM1/SMA	6/4/5	Right supplementary motor area, sensorimotor gyrus	-2	-14	60
latPFC	9/46	Right superior frontal gyrus/lateral prefrontal cortex	30	42	36
-	8/6	Left superior frontal gyrus/SMA	-22	14	52
-	21/22	Left middle temporal gyrus	-62	-30	4
-	44/45	Left inferior frontal gyrus/lateral PFC	-57	18	12
) Contrast for Posture *congruence*					
pTPJ	39	Right temporo-parietal junction: angular gyrus	50	-60	24
SPL(BA40/7)	40/7	Right superior parietal lobule	42	-58	60
SMA	6	Right supplementary motor area	26	-6	64
-	18	Left occipital cortex	-38	-90	8
-	7	Left superior parietal lobule	-30	-62	52
) Contrast for Posture *relevance*					
pTPJ	39	Right temporo-parietal junction: angular gyrus	54	-62	36
SM1	3/4	Right sensorimotor gyrus	52	-18	60
vPMC	6/44	Right ventral premotor cortex	54	6	16
-	18	Right occipital cortex	6	-78	28
-	18/19	Left occipital cortex/lateral occipital complex	-34	-94	-8
verage across the 3 contrasts (top, Fig. 4)					
pTPJ	39	Right temporo-parietal junction: angular gyrus	50	-60	32
-	17	Right occipital cortex	0	-96	-10
-	18/19	Left occipital cortex/lateral occipital complex	-30	-96	-2

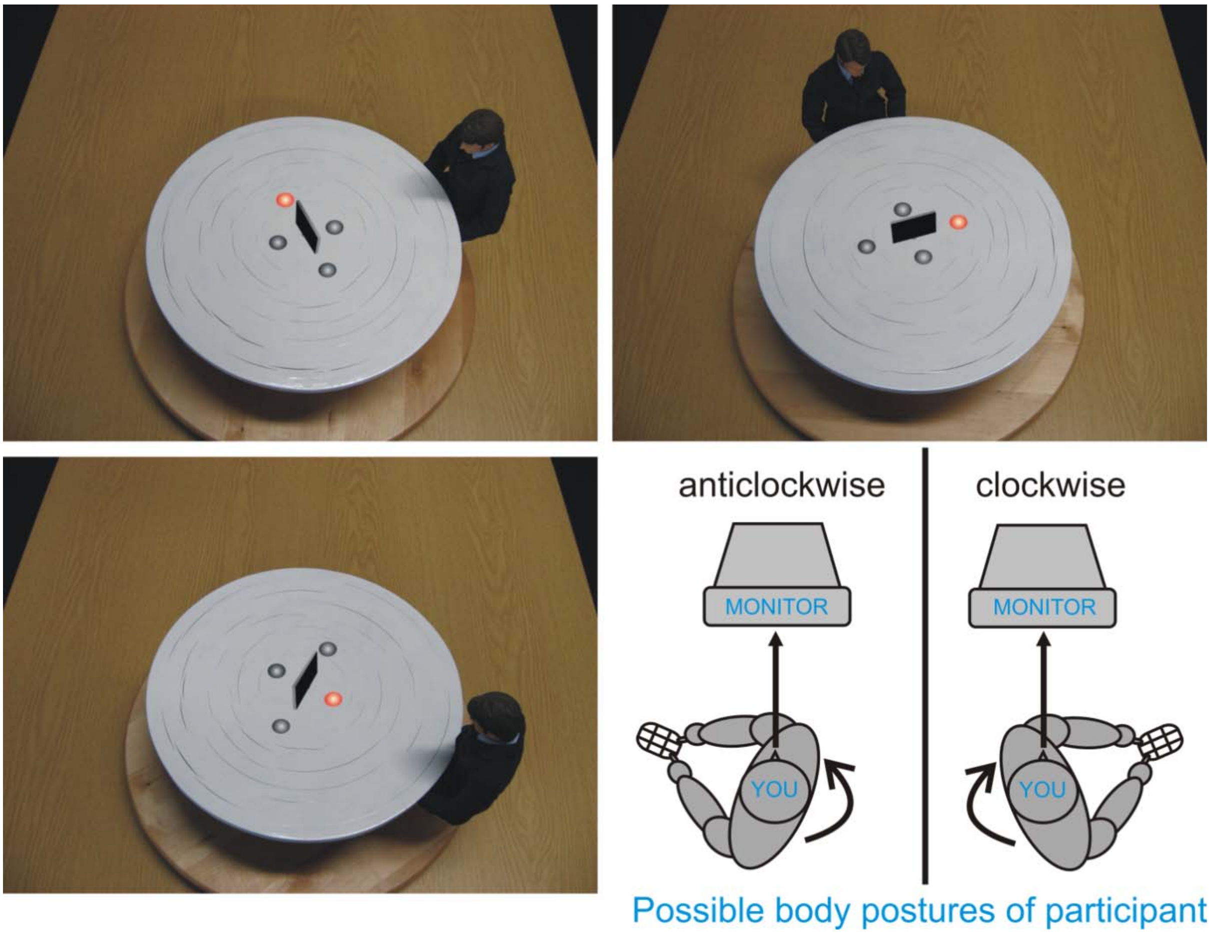

Figure 1: Stimuli and Postures employed by Kessler and Rutherford (2010) and in the current study. Note that images were presented in colour during the experiment and target objects were indicated in red colour (here in white). The top left image shows an example for a “right” target from the avatar’s perspective at 110° anticlockwise angular disparity, the top right image shows an example for a “left” target from the avatar’s perspective at 160° (clockwise), and the bottom left image shows an example for a “visible” target from the avatar’s perspective at 60° (anticlockwise). The bottom right images show the two possible postures of the participant: body turned either clock- or anticlockwise, while gazing straight ahead. Note that this induced either posture congruence or incongruence with the direction of mental self-rotation for any given stimulus. Further explanations in the text.

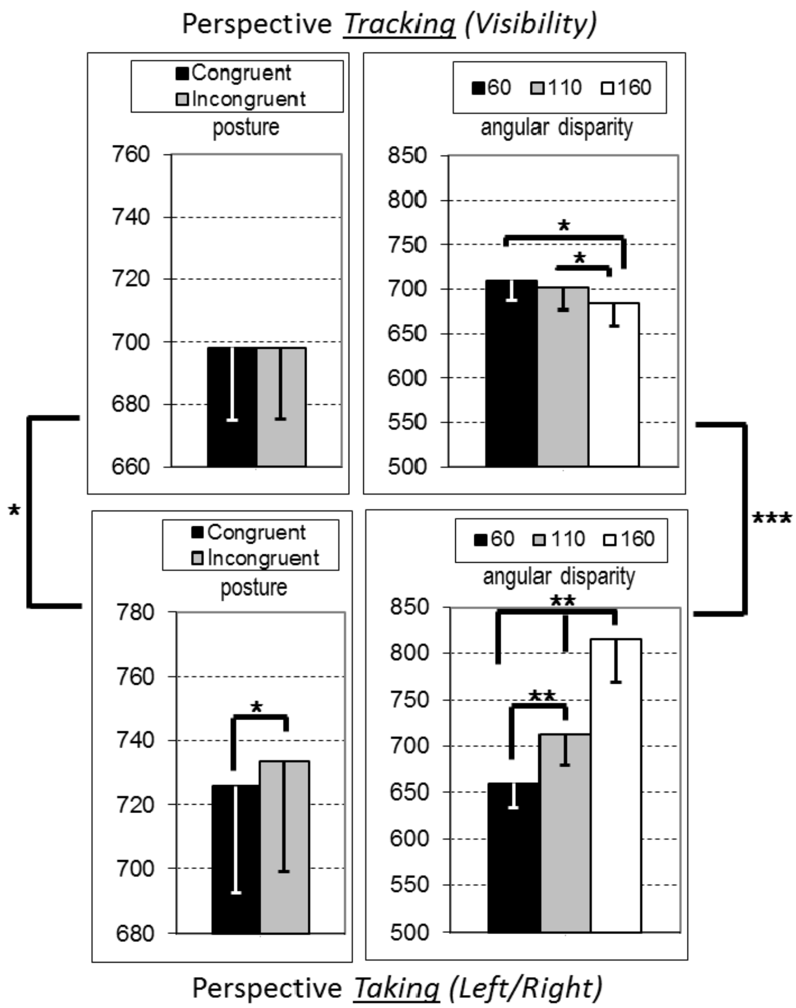

Figure 2: Behavioural effects for response times (RT in msec on the y-axes). Significance is indicated as follows: * = p <.05; ** = p < .01; *** = p < .001. “60”,”110”, “160” refer to the three angular disparities employed in the design (collapsed across clockwise and anticlockwise orientations) and “congruent” and “incongruent” indicate the relationship between the participant’s posture and the target orientation (see also Fig. 1). Error bars denote standard error of mean. Further explanations in the text.

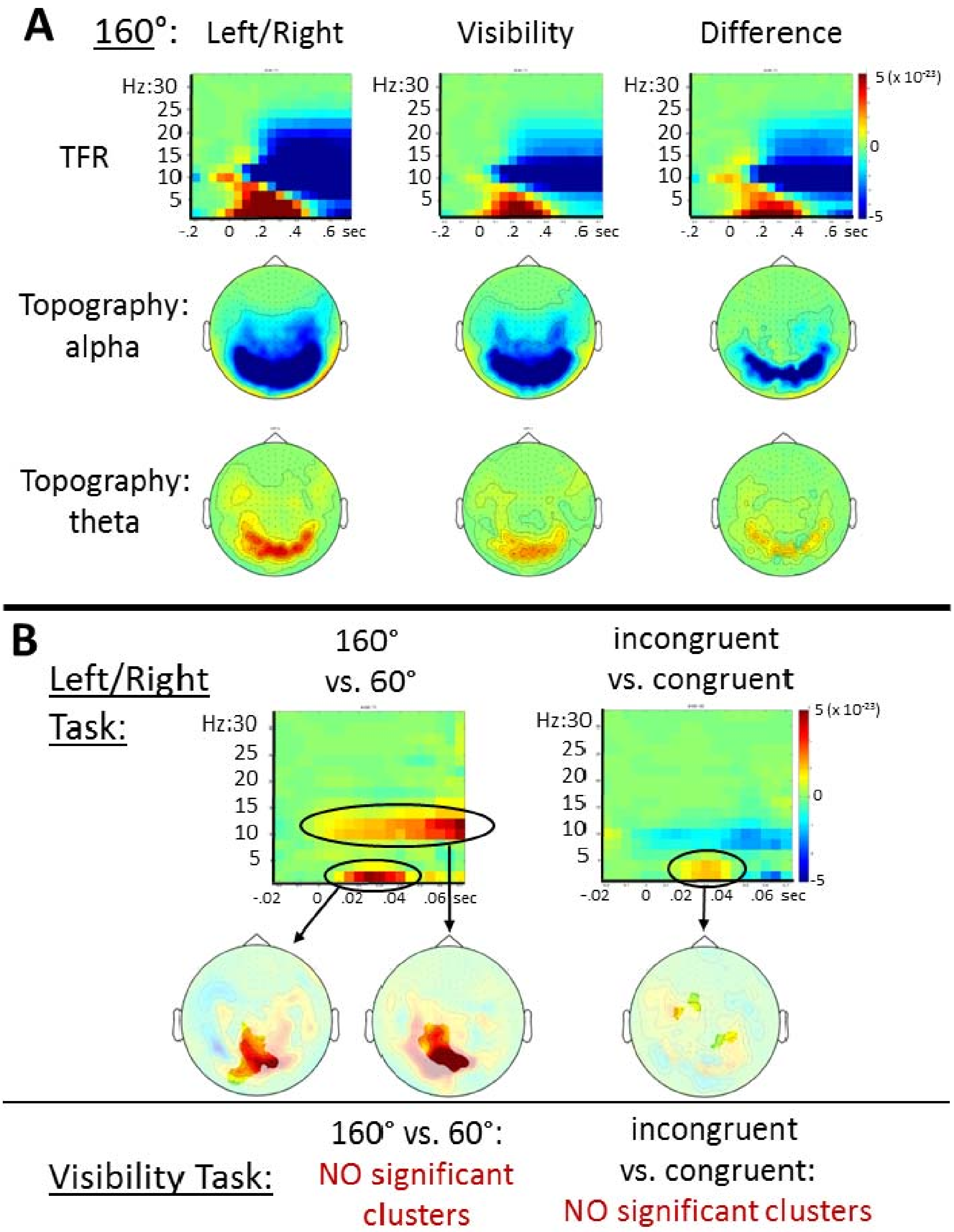

Figure 3: General time-frequency signatures. The top row of Panel A shows typical time-frequency representations (TFRs) for “left/right” and “visibility” judgements at 160° and their difference (left/right - visibility) at the far right, with a theta band increase and an alpha/beta band decrease in both tasks, yet, both frequency effects being more pronounced for “left/right” than for “visibility” (y-axis: 2-30 Hz; x-axis: -200 msec pre-stimulus to +700 msec post-stimulus time; colour-coded scale shows power from $-5x10^{-23}$=blue to $+5x10^{-}$

^{23}=red). Rows 2 and 3 depict the related topographies for the alpha and theta band effects, respectively. Panel B shows two significant TFR cluster effects (for angle and posture, respectively) for the “left/right” task in relation to the pre-trial baseline interval. The TFR graph and topographies on the left show the effect of angular disparity (160° vs. 60°), where 160° reveals a significantly stronger theta increase, while 60° shows a significantly stronger alpha decrease. Note that effects involving 110° angular disparity are shown in Supplementary Material, Figure S2. The TFR graph and topography on the right shows the effect of posture congruence, where a congruent posture reveals a significantly stronger theta increase and a numerically stronger, but non-significant alpha decrease. Topography plots of significant clusters shown below each TFR depict significant channels (and related power topographies) within a cluster ($p < .05$) as fully visible, while non-significant channels are reduced in visibility (70% opaque white). Note that for the visibility task no significant clusters for angular disparity or posture congruence were observed, as indicated at the bottom of Panel B (but see Figure S1 for a pre- vs. post-stimulus comparison for the visibility task, collapsed across all conditions). Further explanations in the text.

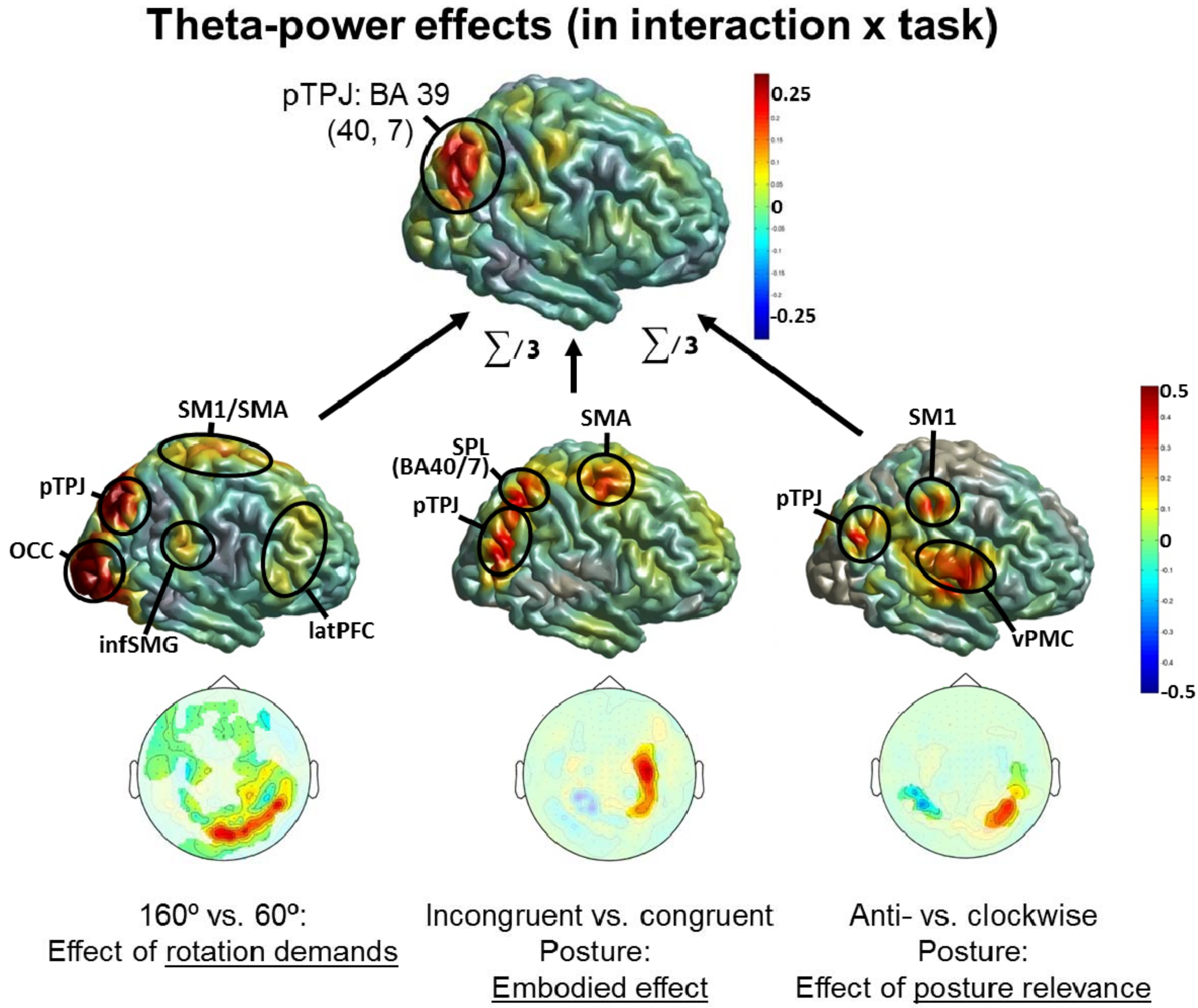

Figure 4: Theta interaction effects in sensor and source space. Three interactions of task (left/right vs. visibility) with 1) angular disparity (160° vs. 60°), 2) posture congruence (incongruent vs. congruent), and 3) posture relevance (anti- vs. clockwise posture). Bottom row: Topographies of interaction effects in the theta band (2-7 Hz, colour-coded scale shows power from $-1x10^{-23}$=blue to $+1x10^{-23}$=red). Significant channels within a cluster ($p < .05$) are fully visible while non-significant channels are reduced in visibility. (For effects at alpha and beta frequencies see Supplementary Material, Fig. S2.) Middle row: Theta power source reconstructions for each of the three interaction effects. TPJ = temporo-parietal junction; OCC = occipital cortex; SM1 = primary sensorimotor cortex; SMA = supplementary motor

area; latPFC = lateral prefrontal cortex; SPL = superior parietal lobule; vPMC = ventrolateral premotor cortex. Colour scale shows normalized theta power (red = positive). Top image: The maximum overlap across the three interaction effects (average) is localised in the right pTPJ, specifically Broadman area (BA) 39, extending into BA40 and BA7. Further explanations in the text.

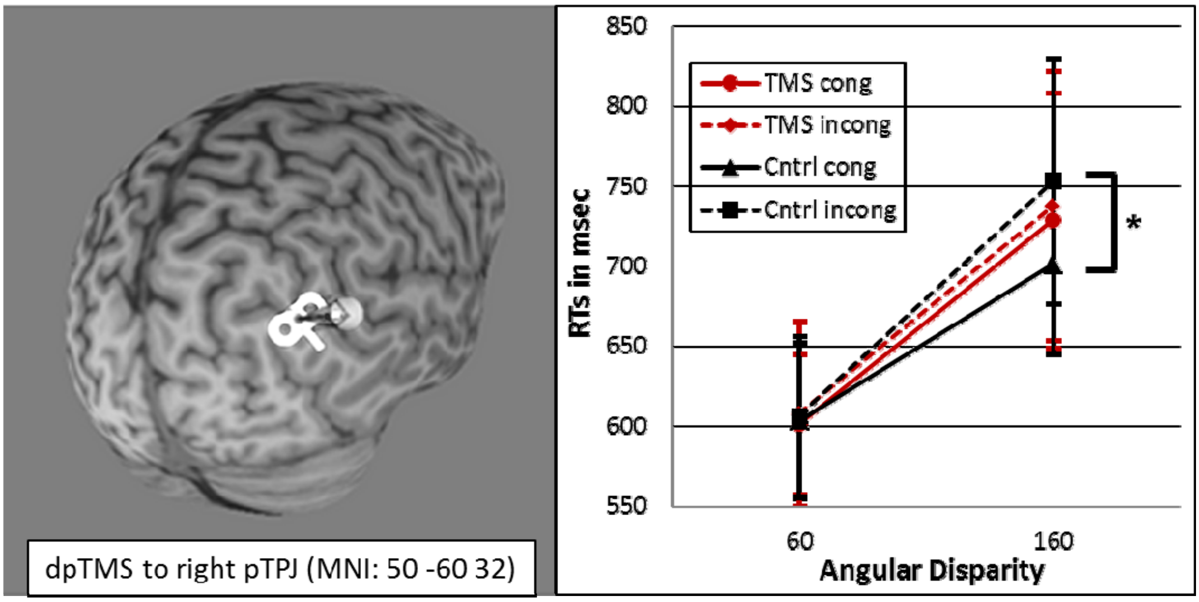

Figure 5: TMS target site and response time results. Left: The same right pTPJ site (MNI coordinates taken from MEG group analysis: 50, -60, 32) was targeted with dpTMS for each individual (MNI normalised) brain using Brainsight®. Right: Response time results, shown as residuals after subtracting a congruent from an incongruent posture for each condition separately (collapsed across clockwise and anticlockwise avatar locations and across left and right targets). The y-axis denotes RT differences in msec and the x-axis contrasts control vs. dpTMS trials for each of the two angular disparities. Error bars denote standard error of mean. Further explanations in the text.